The effect of Photoperiod on the Dimorphism of the Lemon Migrant, *Catopsilia pomona* FABRICIUS

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Introduction

There have been many discussions about whether *Catopsilia pomona* FABRICIUS, 1775 and *C. crocale* CRAMER, 1775 are conspecific or not. In recent years, however, it was found that they are different phenotypes of the same species, because both *pomona* and *crocale* were obtained from the eggs laid by each form (D'ABRERA, 1971; NAITO, 1975; NAITO & IMAMURA, 1978). Nevertheless, the following points have remained unsettled: what is the nature of this variation i.e., is it genotypic or phenotypic, and if the latter is the case, what is the environmental factor involved? Many authors hitherto have expressed various opinions about these problems, which do not seem to be proved experimentally yet (McCUBBIN, 1971; FUJIOKA, 1975; KAWAZOÉ & WAKABAYASHI, 1976; FUKUDA & TANAKA, 1977, etc.). We consider that the dimorphism of this butterfly has some common features with seasonal dimorphism as follows: (1) The two forms show a fairly distinctive seasonal alternation at both northern and southern limits of the distributional range (McCUBBIN, 1971, etc.); (2) f. *pomona* hibernates at Okinawa Is., while f. *crocale* does not seem to do so (FUKUDA & TANAKA, 1977); and (3) f. *pomona* is similar in the general feature of wing markings to the dry-season (winter) form, and f. *crocale* to the wet-season (summer) form, of *Catopsilia pyranthe* L. We investigated the photoperiodic reaction of *Catopsilia pomona*. The result suggested that the occurrence of the two forms was affected by photoperiods and that they were different in the pattern of ovarian development.

Materials and Methods

For a preliminary test young larvae collected at Chinen, Okinawa Is. were used. The main experiments were based on eggs laid by a female collected at the same locality in June of 1977. These materials were sent by air mail to the Biological Laboratory, College of General Education, Kyushu University, Fukuoka, where the experiments were done. Larval food plants were also transported from the same locality. Early stages were exposed to different photoperiods ranging from 10 hr to 15 hr per day in constant temperature cabinets or a room (20±1°C). Two 6 watt

Table 1. Summary of adult dimorphism of *Catopsilia pomona*.

	f. *crocale*	Intermediate form	f. *pomona*
♂. Upperside			
Proximal yellow area	not expanded towards the anal and tornal regions in hindwing, and its outer margin sharply defined in both wings	intermediate	expanded towards the anal and tornal region in hindwing, and its outer margin somewhat diffused in both wings
Marginal fine border in forewing	traceable from base of costa to near vein 2 on outer margin through apex		almost restricted near the apex and macular on outer margin
♂. Underside			
Ground colour	yellowish white	milky white with yellowish tinge	milky white with some yellowish tinge and possessing peculiar lustre
Markings	completely disappearing	weakly developed; discocellular spot not silver in its middle; a series of postdiscal spots weakly appearing	well developed; discocellular spot silver in its middle; postdiscal irregular line sharply defined
♀. Upperside			
Ground colour	milky-white with basal area yellow		yellow
Marginal border in forewing	well developed		weakly developed, but almost disappearing near base of costa
Discocellular spot in forewing.	almost contiguous with costa		completely separated from costa
Marginal border in hindwing	well developed		reduced to marginal vein-dots
♀. Underside			
Ground colour	milky-white to pale yellow		deep yellow
Markings	almost disappearing	intermediate	similar to male, but at apex more strongly developed
Antenna	black		almost red on the dorsal surface

(in the cabinets) or three 40 watt (in the room) "daylight" fluorescent tubes served as light sources, which were operated by time switches. The moisture conditions were not controlled, but a high humidity was avoided in order to lower the larval mortality. Further details of the rearing methods are given in Results. A comparison of ovarian development between the two forms was made using virgin females 4 days after emergence obtained in Experiment 2. Adult females were individually kept in glass jars (9×9 cm) in the cabinet (20 ± 1°C, 14 hr), and fed on diluted honey (about 10 per cent) once a day.

Adults obtained in the experiments were separated into three forms based on the wing coloration and markings, which are summarized in Table 1. The criterion of classification followed that of TALBOT (1939) or SHIRÔZU (1960), etc. based on field specimens.

Results

1. *Photoperiodic response*

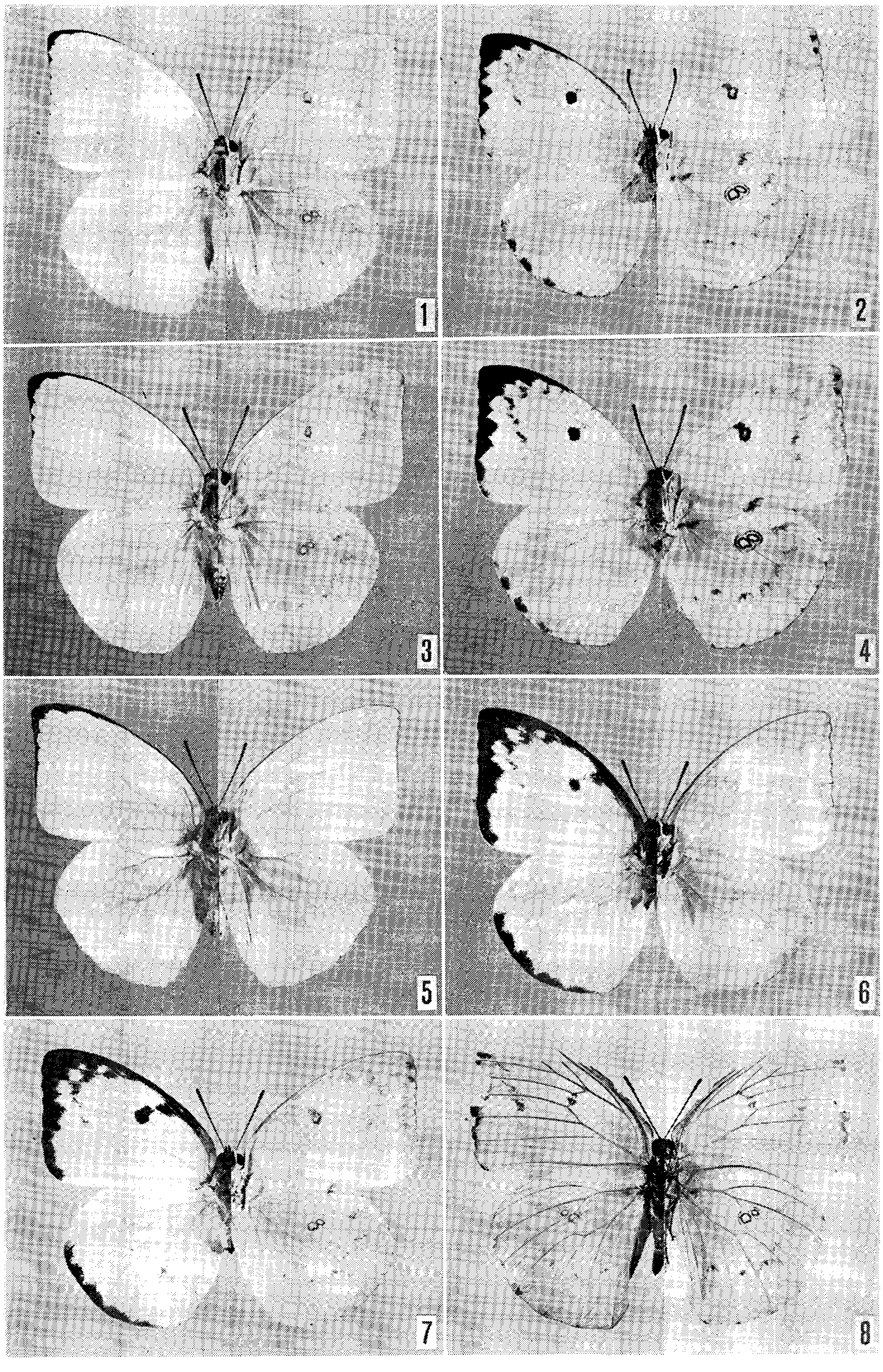
(Experiment 1) Seventy five larvae (2nd-4th instars) collected in the field were used for a preliminary test. They were not considered to be the progeny of a single female. It was assumed, however, that they had been exposed to mean temperatures ranging from 26 to 28°C and photoperiods of about 14 hr, based on the climatic data given in the 1972 edition of Rikanempyo compiled by the Tokyo Astronomical Institute. The larvae were reared on fresh cuttings of *Cassia alata* L. in glass jars (9×7 cm) or transparent cylindrical plastic vessels (10×6 cm). In order to avoid overcrowding, the rearing density was decreased gradually as they grew and kept at 2 to 3 per jar in the last instar. Owing to high larval mortality, adults were obtained only in 10, 13 and 14 hrs of photoperiods. The frequency of each form is shown in Table 2. Most of the pupae at 10 hr produced f. *pomona*, while from those at 13 and 14 hr either

Table 2. Influence of photoperiod at 20 ± 1°C on the form determination of *Catopsilia pomona* collected as larvae in the southern part of Okinawa.

Photoperiod (hr/day)	f. *pomona*	Intermediate	f. *crocale*
10	10	1	0
13	0	0	3
14	0	6	3

Table 3. Influence of photoperiod at 20 ± 1°C on the form determination of *Catopsilia pomona* derived from eggs laid by a female of f. *pomona* collected in the southern part of Okinawa.

Photoperiod (hr/day)	f. *pomona*	Intermediate	f. *crocale*
10	6	0	0
11	6	0	0
12	0	1	0
13	0	0	2
14	0	0	1
15	1	0	0



Figs. 1–7. The forms of *Catopsilia pomona* FABRICIUS emerged in the laboratory: (1) f. *pomona*, (day-length 10 hr), ♂, (2) ditto, ♀, (3) f. *pomona*, (day-length 11 hr), ♂, (4) ditto, ♀, (5) f. *crocale*, (day-length 13 hr), ♂, (6) ditto, (day-length 14 hr), ♀, (7) Intermediate, (day-length 12 hr), ♀. Fig. 8. Mother butterfly used in the experiment (f. *pomona*). Right half of each figure shows underside.

f. *crocale* or intermediates resulted.

(Experiment 2) A second experiment was started with the eggs laid by a single female of f. *pomona*. Each experimental batch was consisted of thirty eggs. The larvae in each batch were reared in two glass jars (9×7 cm) in the young stages, in a plastic box (15×21×8 cm) from the fourth instar to the early fifth, thereafter in a wooden box (21×31×8 cm) covered with a transparent plastic lid. Fresh cuttings of *Cassia fistula* L. were provided as food. The number of individuals reaching maturity was very small due to high larval and pupal mortalities caused by a disease. The results shown in Table 3 generally agree with those of Experiment 1. The pupae at 10 and 11 hrs produced f. *pomona*, those at 12 hr intermediates and at those 13 and 14 hrs f. *crocale*. However, one individual at 15 hr was of f. *pomona*.

2. *Larval development*

Table 4 shows the larval developmental time in each photoperiod. Although some individuals at 10 and 11 hrs grew somewhat slowly, the minimum time from hatching to pupation in each photoperiod was 18 days and the variance of the developmental time seemed to be rather small. Therefore, the influence of photoperiod on the larval development might be slight.

Table 4. Larval developmental periods under different photoperiods.

Photoperiod (hr/day)	days 18	19	20	21	Mean
10	3	1	0	3	19.4
11	1	4	0	2	19.4
12	1	1	1	0	19.0
13	2	0	1	0	18.7
14	1	0	1	0	19.0
15	1	0	1	0	19.0

3. *Ovarian development*

Fig. 9 shows a comparison of ovarian development between the two forms aged 4 days after emergence. It was clear that the ovaries were at a less advanced stage of development in f. *pomona* (4 examples) than in f. *crocale* (3 examples).

Discussion

1. *Photoperiodic reaction and seasonal life cycle*

Although any decisive conclusion cannot be drawn from the insufficient data, photoperiods shorter than 11 hr gave only f. *pomona*, while those longer than 13 hr usually f. *crocale*. Therefore, the critical photoperiod at 20°C seems to lie between 11 and 13 hr. As one individual of f. *pomona* was obtained at 15 hr (which is absent in Okinawa Is.), a quantitative determination of the photoperiodic response curve should be made in the future.* It is, however, quite possible that the adult from is

* In an additional test the larvae were exposed to a photoperiod of 10 hr (17–20°C) in the young stages and transferred to that of 15 hr (20°C) in the last stage. In this case both forms emerged.

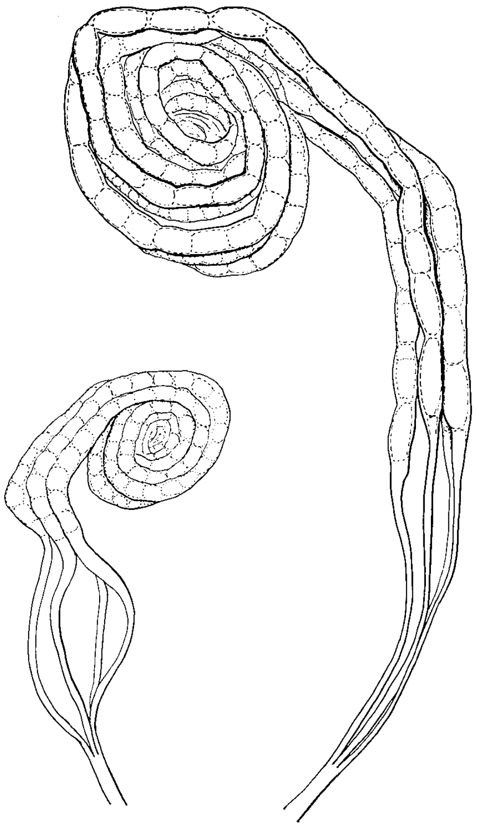


Fig. 9. Comparison of the ovarian development of the two forms 4 days after emergence. The adult females were reared at a temperaure of 20±1°C and photoperiod of 14 hr.

determined mainly by photoperiod, so that we examined the correlation between the seasonal distribution of the different forms and the seasonal changes of day-length.

From Fig. 10 it is apparent that the ratio of f. *pomona* to f. *crocale* is clearly high when the day-length is shorter than 12 hr (from November to February) and low when it is longer than 12 hr (from May to October). A distinctive seasonal alternation of both forms was also found in Clermont (23°S), Queensland, Australia (McCubbin, 1971). In this locality, f. *crocale* appears under the long day-length of summer (December–April), while f. *pomona* under the short day-length of winter (middle of May to September), though they coexist over a considerable period of time. From these data together with the experimental results, the main determining factor seems to be the day-length during the developmental stages at least near the northern limit of the range. As seen in Fig. 10, however, a few individuals of f. *pomona* were found under long day-length. They might represent immigrants from the south, because there are numerous records of f. *pomona* migrants collected in southwestern parts of the main islands of Japan (especially from June to October), while of such records are very few in f. *crocale*.

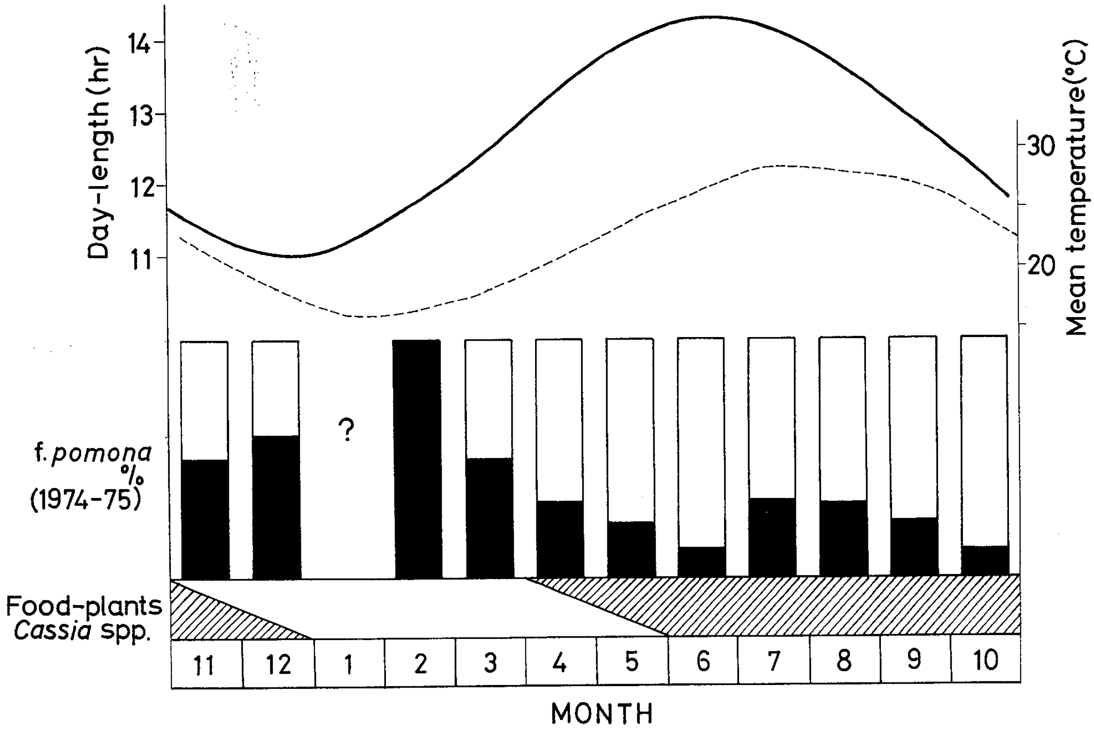


Fig. 10. Relation between the day-length and the seasonal distribution of f. *pomona* in the southern part of Okinawa Is. The day-length is represented by the time from sunrise to sunset plus civil twilight period (30 minutes). The percentages of f. *pomona* (black rectangles) are based on observations or collections in the field (1974–75). The monthly mean temperatures and the occurrence of fresh leaves of food plants (*Cassia* spp.) are also shown. (Somewhat modified from FUKUDA & TANAKA, 1977).

2. *Ecological significance of dimorphism*

FUKUDA and TANAKA (1977) pointed out the ecological characteristics of each form as follows: f. *pomona* is (1) migratory, (2) long-lived and overwintering, and (3) diapausing, while f. *crocale* is (1) less migratory, (2) short-lived and non-overwintering, and (3) non-diapausing. In two Japanese *Eurema* species, *hecabe* and *laeta*, the short-day form (autumn form) undergoes an imaginal diapause and shows the retardation of ovarian development (YATA, 1974). Furthermore, the autumn form of *laeta* moves over a considerable distance in search of a hibernation site (NAKANISHI, 1977). FUKUDA and TANAKA's assumption that f. *pomona* represents the diapausing type may well be supported by its occurrence under short day-lengths and its retarded ovarian development. If f. *pomona* and f. *crocale* represent diapause and non-diapause generations, respectively, the dimorphism of this species would be, at least in the subtropical region, ascribed to seasonal variation; f. *pomona* and f. *crocale* may be regarded as the autumn and summer forms, respectively. In this connection, it should be pointed out that a few individuals of f. *pomona* survive winter (January–March) in Okinawa Is., when fresh leaves of food plants for the young larvae are absent (FUKUDA & TANAKA, 1977 etc.). In Okinawa Is. the form-determination seems to be controlled mainly by the day-length as stated before. At the lower latitudes in

the tropical region, on the other hand, the dimorphism may be due to "phase variation" rather than to seasonal variation. At such latitudes, the eggs or larvae may frequently reach such an extremly high density that the food supply is depleted. The crowded larvae were in fact observed to produced f. *pomona*, while those in a low density resulted in f. *crocale* on July 14, 1970 at Guadalupe Creek, Cebu Is. (Mr. Ban TANAKA, personal communication). Further experiments are necessary in order to prove this assumption.

Summary

Catopsilia pomona FABRICIUS shows two distinctive forms, f. *pomona* and f. *crocale*, and each form had been treated as a separate species till quite recently. In the present study, the effect of photoperiod on the form determination was examined. Larvae derived from a *pomona* female collected at the southern part of Okinawa Is. were reared at a temperature of 20 ± 1°C and photoperiods of 10, 11, 12, 13, 14 or 15 hr of light per day. As the result, all the pupae raised in photoperiods shorter than 11 hr produced f. *pomona*, while most in longer than 12 hr resulted in f. *crocale* or intermediates. A similar tendency was observed in another experiment with wild larvae collected at the same locality. This photoperiodic determination is consistent with the seasonal alternation of the two forms in the field. FUKUDA and TANAKA's assumption that f. *pomona* represents the diapausing type may well be supported by the fact that this form occurs under short day-length and shows the retardation of ovarian development.

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Postscript: After the completion of our manuscript, we found that Yamasaki, H. (1978) had investigated the effect of photoperiod on the dimorphism of *Catopsilia pyranthe* L. using the eggs and larvae collected in the field. His result was that all pupae at 10 hr emerged as the autumn (dry-season) form, while those at 14 hr as the summer (wet-season) form. This is in agreement with our results, though the materials used are different (Yamasaki, H., 1978. Relation between seasonal forms and day-length in *Catopsilia pyranthe* L. *Kontyû to Shizen*, **13** (6): 28–30. In Japanese.)

抄　　録

ギンモンウスキチョウ *Catopsilia pomona* Fabricius とムモンウスキチョウ *C. crocale* Cramer が同種か別種かについては長い間意見がわかれていたが，D'Abrera (1971) や内藤・今村 (1976) の飼育・観察により，これらが同一種の異なる表現型にすぎないことが実証された．しかし，この2つの型が遺伝的な多型なのかそれとも非遺伝的なものなのか，そしてもし後者だとすればその決定要因は何なのかという点に関してはまだ解明されていない．筆者らはこの点を明らかにするために本種の光周反応を実験的に調べてみた．

材料はすべて沖縄県知念村において，1977年 6～7 月に採集されたものである．実験は福岡の九州大学教養部生物学教室で行なったため，材料および食草は沖縄から空輸のものを使用，幼虫の飼育は 20±1°C 恒温，日長 10～15 時間の条件下で行なわれた．

最初の予備的な実験では野外でランダムに採集された幼虫 (2～4 令) を用いたため，それらの母蝶の由来は全く不明である．しかし 10 時間日長区ではほぼ 100% のギンモン型が生じ，13, 14 時間区では全くギンモン型は得られず，ムモン型および中間型が生じた．次の本実験では1頭のギンモン型♀から人工採卵した卵を用い，採卵直後からただちに光周処理を行なった。その結果は予備実験とほとんど一致し，10, 11 時間日長区では 100% ギンモン型，12 時間区では中間型，13, 14 時間ではムモン型が得られた．ただし，15 時間日長区で羽化した1頭はギンモン型であった．一方，幼虫の発育期間は各日長区ともほとんど差異がなく，平均 19 日であった。本実験で得られた未交尾♀成虫を 20±1°C, 14 時間日長の条件下で飼育し，羽化後4日目に卵巣を解剖した結果，ムモン型ではかなり卵巣の発達がすすんでいたが，ギンモン型はほとんど未発達であった．

福田・田中 (1977) による沖縄県南部における本種の採集・目撃データーをもとに，両型の発生消長と自然日長の変化との関連性を検討した結果，日長が 12 時間以下の短日期 (11～2 月) にはギンモン型の比率が高く，日長が 12 時間以上の長日期 (5～10 月) には逆にムモン型の比率が高いこと

がみいだされた。これらの観察結果と筆者らの得た実験結果から判断すると，少なくとも本種の分布限界にあたる高緯度地域では，型決定の主要因は幼虫期の日長であろうと考えられる．また，ギンモン型の卵巣発育に遅延がみられることから，本種の多型現象はキチョウでみられた季節的多型とかなり類似した性格をもち，従って福田ら (1977) が指摘したようにギンモン型は成虫休眠型，ムモン型は非休眠型を代表しているように考えられる．しかし一方，熱帯を中心とした低緯度地域では季節的多型の性格よりもむしろ相変異的な性格をあらわすように思われる．この点を示唆する事実として，熱帯地域では本種の卵や幼虫がしばしば著しい高密度となり，*Cassia* 属の木に大害を与えることが挙げられる．